

MANUAL I

PRINCIPLES OF COMMERCIAL POULTRY BREEDING



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I. MICHAEL LERNER

Principles of
**COMMERCIAL
POULTRY
BREEDING**

A semi-technical account of recent developments in genetics applied to breeding for the improvement of economic traits in poultry. For the breeder, the hatcheryman, and the commercial poultryman.


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This manual outlines the current status

of the techniques of commercial poultry breeding in the light of recent developments in genetics and applied animal breeding. It is now half a century since the basic principles of inheritance were recognized. Since then the advances made in fundamental genetics have been reflected in the theory and practice of breeding only to a limited extent. The general scheme of transmission by inheritance of characters which can be classified as simply present or absent in a bird (like "rose comb") has been fully understood and exploited by many practical breeders. But the problem of breeding for economic traits like egg production, whose expression is usually *continuous*—that is, not naturally falling into a few classes such as are formed by the more common comb types—has been a difficult one to solve. It is not that breeding methods have not been successful with such characters. The difficulty has been in making them efficient, and putting them on a quantitative basis.

Although the genetic principles of the inheritance of continuous traits were formulated some years ago, they have only recently been applied to economic characters. The method involved calls for a somewhat different outlook than we have used in the past. This manual has been written to explain it.

There is no denying that the more we learn of a biological subject the more complex it becomes. Commercial poultry breeding is no exception. Understanding the reasons and implications of many statements to be made in the course of our discussion may require an advanced statistical and biological training. To make this manual useful to the commercial poultryman at large as well as to the hatcheryman and specialized breeder, you will be asked to accept some statements on faith. No matter what old-fashioned practitioners had to say to the contrary, breeding is a mathematical process. It is impossible to eliminate mathematics from a full discussion of the subject. But formulas can be held at a minimum if you are willing to accept a few without

proof. The specialist who wants to verify the conclusions to be brought out may consult the vast and intricate literature on the subject, which is scattered in many of the technical journals. If others remain unconvinced, they will have to seek remedy by becoming specialists themselves.*

* References to the many contributions to the subject of genetics in relation to animal improvement have been omitted for the sake of readability. A few suggestions for further reading will be found on page 47. I am glad to record here the names of three geneticists on whose theoretical work much of the discussion to follow is based. They are Sewall Wright of the University of Chicago, R. A. Fisher, now of the University of Cambridge, and J. L. Lush of Iowa State College.

The Genetic Background

The Basis of Inheritance

The unit of inheritance in all forms of plant and animal life is the *gene*. The nucleus of each sperm and each egg contains an assortment of threadlike bodies known as chromosomes, which are composed of genes. Fertilization involves the union of a sperm and an egg nucleus, so that the newly arisen individual possesses two sets of chromosomes, and therefore a pair of each of the different genes. Half of the inheritance thus comes from the sire and the other half from the dam, and all the body cells normally contain within their nuclei representatives of both paternal and maternal genes in paired form. When the individual itself starts producing germ cells, a regular process of reduction of chromosome number happens. Thus the number of chromosomes entering each germ cell is half of that found in body cells. The identity of the paternal and maternal set of chromosomes is not preserved in this process, so that the chromosomes are re-sorted in each generation.

There are 39 chromosome pairs in each cell of a chicken. One member of each pair is derived from the sire and the other from the dam. The bird itself will contribute 39 single chromosomes to its own offspring, but which of them will be of paternal and which of maternal origin is determined by chance.

Sex Linkage

One member of the set of 39 behaves differently. It is called the sex chromosome. The male has a pair of these, the female a single unpaired one. When the germ cells of the female are formed, half of them will each contain one set of 39 chromosomes. The other half will each contain 38 of the regular chromosomes but will lack a sex chromosome. If a germ cell of the first type is fertilized, the new individual will be a male, since it will contain a pair of sex chromosomes in addition to the regular set of 38 pairs. If an egg of the second type (lacking a sex chromosome) unites with a sperm, the new individual will be a female: it will once more contain 38 pairs and an unpaired sex chromosome.

Genes carried on the sex chromosome are called *sex-linked*. They differ from the others (autosomal genes) in that, as above, a female receives her complement of sex-linked genes only from her sire, and in turn transmits them only to her son. A male, on the other hand, receives one set of sex-linked genes from each of his parents and similarly transmits a full set to both his sons and daughters.

Homozygosity and Heterozygosity

When any given gene pair contains identical members, that is to say when the member of the pair contributed by the sire is the same as the one contributed by the dam, the individual involved is said to be *homozygous* for that gene. When the two genes are different, the individual is *heterozygous*.

Genes are commonly designated by letters. Different members of a given gene pair are distinguished either by using capitals for one and lower-case letters for the other (like R and r), or by subscripts (like A_1 and A_2). Thus for a given gene pair A , it is possible that the bird received from its father the gene A_1 , while the mother contributed A_2 . The heterozygous bird will have the constitution A_1A_2 . A homozygous bird may be of the constitution A_1A_1 or A_2A_2 . In the course of germ-cell formation, only one member of the pair will enter each sperm or egg. Hence heterozygotes will pass A_1 to one half of their offspring, and A_2 to the other half. Homozygous birds will, however, produce only one kind of germ cell: if their constitution is A_1A_1 it will be A_1 ; if A_2A_2 , it will be A_2 .

When a character depends for its expression on a single gene pair, whose effect is not greatly modified by environment, we can often distinguish the two types of homozygotes from each other and sometimes from the heterozygote. Take plumage color in the Blue Andalusian fowl. The two homozygote forms are respectively black (A_1A_1) and blue-splashed white (A_2A_2), while the heterozygote (A_1A_2) is blue. We can readily see that homozygous birds mated within their own type will breed true. Two homozygotes of contrasting types mated to each other will always produce heterozygous offspring. The blue birds, being heterozygous, can never be true-breeding. Their eggs will be of two kinds, A_1 and A_2 . Each of these has an equal chance of being fertilized by its own or by a different kind of sperm. Thus on the average, one quarter of the offspring will be black, one quarter white, and one half blue, as the following diagram shows.

		Kind of eggs	
		A_1	A_2
Kind of sperm	A_1	A_1A_1	A_1A_2
	A_2	A_1A_2	A_2A_2

Among every four offspring the average ratio will be one A_1A_1 : two A_1A_2 : one A_2A_2 .

Dominance

There are other cases where one kind of gene may be *dominant* to the other of the pair. Here the heterozygote will not be distinguishable from the dominant homozygote.

Thus we may designate a pure-breeding rose-combed bird RR , indicating that it has a pair of identical genes. A single-combed bird will be of the constitution rr . It possesses a pair of *recessive* (r) genes. The crosses between these types will be heterozygotes (Rr) but will exhibit the dominant trait. In other words, an Rr bird cannot be distinguished by its appearance from RR birds, since it will also be rose-combed. But the breeding behavior of the two types will be different. When an RR bird is mated to an rr bird, all of the first generation offspring will be rose-combed as indicated. But among the first generation progeny of an Rr bird mated to single-combed birds (rr) one half will be rose-combed and one half single-combed:

		Kind of germ cells produced by Rr birds	
		R	r
Kind of germ cells produced by rr birds	r	Rr	rr

On the average, half of the offspring will be Rr and half rr .

This example demonstrates that the appearance of a bird (its *phenotype*) may be different from its breeding potentialities, that is to say from its actual genetic makeup, or *genotype*. Here the difference is caused by the phenomenon of dominance. There are other and more usual reasons why the correspondence between phenotype and genotype is not perfect.

Genetic and Phenotypic Variation

Suppose we are dealing with a quantitative character such as body weight. The number of gene pairs contributing to it is probably very large. Ordinarily, when more than two or three gene pairs are involved in the inheritance of a character, it is unprofitable and almost impossible to isolate and measure the effects of each. We have no way of writing out the genetic constitution of any given individual for body weight in the way we have for comb shape. We can weigh a bird and determine that it has a phenotype of three pounds, five pounds or whatever it may be for any specified age.

The phenotype is the product not of the bird's genetic constitution acquired from its parents, but of the interaction between its genes with various non-genetic or environmental forces. The more the actions of the genes involved are susceptible to environmental modification, the less accurate will be our judgment as to the bird's actual genotype.

Statistical methods have been devised to measure approximately what percentage of the variation of a given character is due to genetic forces and what to environmental influences. In body weight, the percentage of genetic variation is about 40 per cent, and the environmental percentage about 60 per cent. The statistic expressing the percentage of genetic variation is known as the *degree of heritability*. Heritability for body weight is thus about 40 per cent, usually written .40.

Heritability

The degree of heritability is an exceedingly important figure for us. It determines the amount of gain which breeding selection can accomplish. More important, its magnitude governs the choice of an efficient selection method. So it is vital to understand what heritability (we shall call it h^2) actually means.

Heritability does not mean that 40 per cent of a given animal's body weight is due to heredity and 60 per cent to environment. What the statement that for body weight h^2 approximates .40 means is this: that in a population of birds there will be differences between individuals, partly caused by the fact that each bird has a somewhat different genetic constitution, and partly by the fact that each bird has been under an environment to some extent peculiar to itself; the degree of heritability is the fraction of the total of such individual *variation* which is traceable to genetic differences. For body weight this fraction is roughly 40 per cent.

Standardizing Heritability. If the birds in a population are deliberately subjected to different environments, the total variation among them will be increased. But the absolute amount of genetic variation will remain unchanged. In other words, heritability will drop. If we call the genetic variation G , and the environmental variation E , the degree of heritability will be

$$h^2 = \frac{G}{E + G}.$$

Suppose by manipulation of management the amount of E is doubled. The degree of heritability in this new population,

$$h^2 = \frac{G}{2E + G},$$

will now be obviously less than it was in the first place.

In order to have a uniform standard for heritability, it therefore seems best to use the term to mean the relative amount of genetic variation *when the environment is uniform or random for all the birds in a population*. This means that the E fraction of the total variation will be due to *uncontrollable* environmental differences. Hence, when we say that body weight has a heritability of .40, we mean that when all the birds in a population are raised and kept in the same houses, are given the same diet, and in general are subjected to uniform treatment, 60 per cent of the total variation is still not traceable to genetic differences between them. This fraction then must be due to developmental accidents and deviations, to noninherent peculiarities of individuals, and to other sources of this kind.

The conditions of genetic variation must also be standardized. We have shown that it is possible to double the E fraction by manipulation of environment. It is also possible to modify (either increase or decrease) the absolute amount contributed by the G fraction to the total variation.

Suppose the population we deal with consists entirely of full sisters or brothers. The amount of genetic variation in such a population will be much less than in an ordinary flock of chickens which contains full sisters, half sisters, cousins, less closely related individuals, and some with no common ancestors for many generations. This should be clear from the fact that full sisters have more genes in common with each other than unrelated individuals. Some genes will be held in common by all birds in a flock. Genetic relationships are measured from a base representing the average proportion of genes common to all members of a population and taken as zero. If we say, then, that two non-related individuals have a genetic relation of zero, and that animals with exactly the same genetic constitution (such as identical twins in mammals) bear a genetic relation to each other of 1, full sisters are related to each other to the extent of .5.

In a group of full sisters, then, the amount contributed to the total variation will be $\frac{G}{2}$ as compared to G in a random-bred population. The degree of heritability in this restricted population will be

$$h^2 = \frac{G/2}{E + G/2}.$$

The same principles apply to any population in which the amount of genetic variation is reduced by such means as inbreeding. Conversely, the G fraction may be increased in a population created by a mixture of completely unrelated inbred lines of the same breed, or by a mixture of different breeds.

We therefore adopt another convention to standardize the meaning of the term heritability. By the degree of heritability we mean the proportion of the variation which is genetic in a *random-bred* flock, that is to say, a flock

in which males and females are mated together without regard to their genotypic or phenotypic resemblance to each other. Heritability determinations made on a different basis can be statistically reduced to such a common form. The heritability estimates we shall make later for various traits have been so reduced.

It should be clear now that what the degree of heritability measures is the accuracy of identification of the genotype from the phenotype, or the correlation between them. The higher the heritability, the greater is this correlation. If the heritability of a character is 100 per cent (or 1 in our terms) it means that the genotypic value of a bird coincides with its phenotypic value. At the other extreme, a heritability of zero would mean that the genotype and phenotype are not at all correlated: that all of the variation in the phenotype is due to non-genetic or environmental sources.

Measuring Heritability

It may be easier to get the idea of heritability if we give a simplified example of one method of computing it. Suppose in a random-bred flock we have several groups or families of full sisters as well as a number of half-sister families (birds from different dams but sired by the same male). We have already noted that the genetic relationship between full sisters is equal to .5. The similar figure for half sisters is .25. If we have body weights, for example, for all of the birds in the flock, we will note that those of full sisters will resemble each other more than those of half sisters do. As a matter of fact, the genetic resemblance between the former will be twice that between the latter, because as indicated by the respective genetic relationships, full sisters have twice as many genes in common as half sisters (that is, twice as many of the genes which are not common to the whole flock).

The phenotypic resemblance within any group of birds can be computed from measurements on them by means of what is known as the *coefficient of correlation*. Now if we find that the coefficient of correlation for body weight between full sisters is .2 and between half sisters .1, we can attribute the difference (.1) to the fact that the genetic relationship in the first case was .5 and in the second .25. Thus, for every .25 difference in the genetic relationship, there is a difference of .1 in the phenotypic correlation coefficient. The figure .1 corresponds to one quarter of those differences between phenotypes of completely unrelated birds which are due to differences in their heredity. All of the genetic difference between them is then four times this fraction. In other words, the heritability of body weight is $4 \times .1$ or .4.

So far we have considered the total phenotypic variation in terms of its two components, genetic and environmental. Each of these can be subdivided

further. The full complexities of the situation would take us far afield, but two points must now be made because we shall need to refer to them in our later discussion. One refers to genetic variability and the other to environmental variability.

Non-Additive Genetic Variation

We have assumed that the action of genes is additive. This means that if gene *A* has a given effect on the trait in question, a bird having the genetic constitution *AA* will show twice the effect. To say it in another way, bird *AA* will be as different from bird *Aa* as the latter will be from bird *aa*. Additiveness also means that for two or more gene pairs, the combined effects will equal the sum of the individual effects. Take two pairs of genes, *A-a* and *B-b*, for which the differences between the effects of the capital-letter and small-letter genes are equal. The bird possessing the genetic constitution *AAbb* will be superior to one of the genotype *aabb* by a certain amount. The amount will equal the difference between birds *aaBB* and *aabb*, since we assumed that the differences between *A* and *a*, and between *B* and *b* are equal in effect. The additive idea means that genotype *AABB* will be superior to *AAbb*, *AaBb* or *aaBB* to the same extent that each of them is superior to *aabb*.

Dominance and interaction between different gene pairs may interfere with additive gene action, but it so happens that the idea of additiveness seems reasonably well justified for many quantitative traits in random-bred flocks, at least in such flocks at lower levels of performance. However, when intensive inbreeding is practiced, or after a long period of selection, nonadditive gene effects apparently become significant.

The difference in the two situations means in practice that whereas in average random-bred flocks, knowledge of the genotypes of two prospective parents permits the prediction within certain limits of the performance of their offspring, in the case of matings between inbred birds, or birds at upper levels of improvement, such prediction is usually not possible.

The C Effects

We have shown that one of the ways of determining the degree of heritability depends on the closeness of resemblance between full sisters, as compared to that between half sisters. It was assumed that the difference between the two is due to the fact that full sisters hold more genes in common than half sisters. But they may also resemble each other more because, being full-sister embryos, their pre-hatching environment was supplied by the same dam, while half sisters were provided with an embryonic environment by different hens. If such additional differences exercise significant effects, we

may have included in what we assumed to be net genetic differences also some environmental differences.

We designate environmental differences of this type as environmental effects common to members of the same family, and assign to them the letter *C*, in the same way as we assigned *G* to genetic differences and *E* to uncontrolled environmental effects. Besides strictly maternal influences, the *C* fraction may include other effects when, for instance, members of each family are housed separately, and thus subjected to non-random environment.

So far few *C* effects have been found for chickens when all birds irrespective of family origin are housed together. For instance, with respect to body weight, although the *C* factor is great at hatching time (because of the egg size characteristic for each given dam, which exercises such powerful effects on the weight of day-old chicks), by the time the birds reach maturity it is only about 5 per cent. More significant *C* effects however are apparent in egg traits, such as shell thickness, and possibly in percentage of firm white. We shall later come back to the problem of the *C* fraction.

Heritability and the Fixation of Characters

The heritability concept has an important application to the possibility of fixing desirable characters in a flock. In the early days of Mendelian genetics, it was assumed (and many still believe this) that if all the genes controlling a given trait were identified, it would be possible to produce by selection a completely uniform flock with respect to their performance for this trait. It became known somewhat later that this objective cannot be accomplished by selection alone and that intensive inbreeding must be brought into play. But we can now see that even if inbreeding is carried to the point where every bird in the flock is of exactly identical genetic constitution, uniformity of performance will not follow.

The genotype determines only the hereditary part of the variation and not the environmental part. If, for body weight, we were to remove all the genetic sources of variation, 60 per cent of the original variation in phenotype would still be exhibited in the genetically uniform group of birds (h^2 being .40). Many other productive traits have an even lower heritability than body weight. Only a minor fraction of variability in them can be removed by inbreeding. There are other aspects of inbreeding which we shall mention later. But we may say at once that not only the possibility but even the desirability of complete uniformity is doubtful. A flock of birds all possessing identical genotypes cannot be improved further by genetic means. Of course, if their genetic constitution is the best possible, they need no further improvement. But the difficulty is that there is no such thing as the *best possible* genotype for *all* environments.

Suppose a slight change in the environment occurs, such as the onset of a hitherto unexperienced disease: the genotype which was superior in the previous environment will no longer be superior in the new. Attainment of complete uniformity thus destroys the flexibility of a population, making it rigid and unadaptable to any unpredicted changes of environment. When uncontrolled environment plays such a dominating role in determining phenotypic levels of performance, as it does in the case of economic characters, the objective of complete genetic uniformity cannot be a wise one. Eventually, perhaps, methods will be discovered to overcome this difficulty (for example, a complete control of environment). But today a genetically flexible flock is both the desirable one to have and the only practicable kind.

The Breeder's Tools

There are three and only three ways in which a breeder can contribute to the genetic improvement of his flock. First, he can decide which birds of those available will become the parents of the next generation. This is *selection*. Second, it is in his power to decide which particular male will be mated to any given female. This involves a choice of a *mating system*. Third, he can within certain limits determine what proportion of the next generation will originate from each of the birds selected to be parents. This is his power to control *reproductive rates*.

For our purposes, reproductive rates may be included as part of selection. Although theoretically the breeder can decide to have a variable number of offspring from each mating in the next generation of his flock, in practice it is simpler to permit free and unrestricted reproduction of the chosen parents throughout the length of the normal hatching season. Only occasionally is it worth while to produce an extra hatch or two from part of the selected group of birds. Such a procedure will lead to confusion if followed too often, because the environmental effects of out-of-season hatching may make comparisons difficult between the performances of birds widely differing in hatching date. Late-hatched birds from superior families may, of course, be profitably used in a hatchery flock for production of commercial breeding stock. Measurements on such birds however are of restricted value.

Another way of controlling reproductive rates, besides extending the hatching season, is to repeat the same matings in successive years, so that the repeated pairs of parents will contribute more descendants to following generations than unrepeatd ones. The decisions to be made about repeating birds previously used as parents are really a matter of selection. Perhaps the basis of selection in such cases is different from that used for birds previously not mated. But it is still a question of selection, and to some extent of mating system (page 31).

Selection

In practicing selection, the breeder may choose the parents of his next year's flock either from his own breeding stock or from someone else's. Our discussion will limit itself to the first of these methods. A word about the second—*migration*—will explain why we will not be concerned with its details.

Migration

The use of breeding stock produced outside the breeder's own flock involves what is known in genetics as migration. Each *closed* flock (a flock reproduced entirely from its own members) contains within it an assortment of certain genes, desirable, undesirable, and indifferent, so far as their effect on the character selected is concerned. The task of the breeder working with such a flock or *isolate*, as it is called, is to increase the concentration of the desirable genes at the expense of the undesirable ones. When stock from another isolate is introduced, different genes from those already present in the home flock may be brought in, or more likely the proportions of the same types of genes may change rapidly. In either case, instead of a continuous increase in frequency of desirable genes or wanted genetic combinations, a certain discontinuity results. Since there is no way to identify the new genes, products of the introduced germ plasm must be subjected to the same performance tests applied to the original birds. In this way selection is made operative on the migrants before their contributions are fully incorporated in the fund of genes already present.

In general, it can be shown that the most efficient way to improve the total population genetically is to maintain a large number of non-interbreeding flocks. Application of proper selection procedures and mating systems within each flock will lead to a rise in average genetic quality. Then, occasionally, when rate of improvement within a given isolate slows down or stops because of the exhaustion of potentialities for improvement, an introduction from another isolate can be made, and a similar process of upgrading once more undertaken. Migration should thus be an exception rather than a rule, and the selection principles which are appropriate to the breeder's own stock should be similarly applied to the introduced migrants.

Systematic crossbreeding may be a good method of producing commercial stock for specific purposes (e.g. broiler production), but it is not a technique for genetic improvement. A crossbred generation may be superior to its parents, but the superiority achieved is a dead-end one: it cannot be utilized for further improvement. Naturally this refers to the scheme of crossing breeds, strains and lines afresh every year, and not to methods which

involve crossbreeding for foundation and continued selection from the closed group for the purposes of synthesizing a new breed, variety, or strain.

To return to selection, the general problem presents two aspects: **1**, the choice of animals upon whose performance judgment with respect to any given individual will be based (see below); **2**, the choice of measurements to be made on these animals (page 21).

Types of Selection

So far as the choice of animals is concerned, there are three bases of selection: *mass*, *pedigree*, and *family*. The first is also known as *individual* selection. It refers to the simple evaluation of the breeding worth of birds from their own phenotypic performance on the trait actually selected for, or with respect to some other character. Thus in attempts to improve egg production by breeding, mass selection for females can be conducted on the basis of their trapnest records. The mass selection of males (and of course, if desired, of females) can be carried out on the basis of breed type, health, body weight or characters other than the egg record itself.

The method of pedigree selection makes use of information on the ancestors of the animals to be chosen. Whereas mass selection can be carried out without knowing the identity of a bird's parents, pedigree selection (as well as family selection) requires that the ancestry of the birds in the flock should be known. The simplest form of pedigree selection considers the bird's parents. More elaborate schemes may call upon information about grandparents or more remote ancestors. We need not consider this method in too great detail, because by comparison with the others it is not very efficient.

It is true that in the past (and even today in many animals) pedigree selection has been extensively used. The idea of blood lines, so much beloved by the breeders of racehorses and to some extent of cattle, is founded on this type of selection. Even in poultry one can often find breeders wasting their time in constructing pedigrees carried back 20 or more generations, in the belief that knowledge of remote ancestry is an aid to judgment of the breeding worth of an individual. In sexual reproduction, however, the contribution that each given ancestor makes to an individual is on the average cut by half in every generation intervening between them. Thus an ancestor five generations removed can be expected to have contributed on the average approximately only $3\frac{1}{4}$ per cent of the bird's genes; an ancestor removed ten generations will have contributed less than one-tenth of 1 per cent of the total hereditary makeup of the individual (unless it appears in the pedigree many times). Surely such a small fraction of the genetic constitution can add little to the accuracy of judgment of the bird's genetic merit.

It may be argued that each of the parents contributes half of the genes comprising the genotype of the bird, and so should be of great value in assessing the individual's worth. But it must be remembered that knowledge of the phenotypes of the parents is a different thing from knowledge of their genotypes. The phenotype is determined partly by heredity and is useful to the extent that it is; but if we are to judge by the phenotype, the individual itself is more useful than even its immediate ancestors (except in such cases as egg number in males, for which there is no phenotype). If we decide to bring into consideration the genotypes of parents rather than their phenotypes, we are not using simple pedigree selection, but family selection in one or another form, because more accurate information on genotypes can usually be obtained by consideration of the performance of the bird's relatives.

Family selection is of two types. We can evaluate the respective genotypic merits of a series of birds, first by the performance of their collateral relatives, sisters, brothers, half sisters or individuals of different degrees of relationship, or second, by the performance of descendants. Of the first kind of family selection only full sister or brother and half sister or brother performances offer worthwhile opportunities. The comparatively low degree of genetic similarity between more remote relatives introduces too much inaccuracy to be very useful. The second kind of family selection will be recognized as the progeny test. Before considering full- and half-sib testing (sib is a word meaning sister and/or brother) separately from progeny testing, we will deal first with the general merits of family selection (or family testing).

Our special interest is in the comparative advantages of individual selection and family selection. They can be used separately or in combination. By considering the properties of each we should be able to decide under what circumstances does one or the other or a combination of both provide for the most efficiency.

The Efficiency of Individual Selection

We have noted that the degree of heritability indicates the accuracy with which the genotype can be identified from the phenotype. Now it must be realized that genetic improvement depends on the breeder's skill in choosing for reproduction the superior genotypes present in his population. Only that part of the phenotypic excellence which is due to genetic causes is transmitted from generation to generation. It then seems fairly obvious that the rate of improvement obtained by individual selection is a direct function of the degree of heritability.

Suppose that out of a population averaging 2000 grams in body weight (we may forget the difference in size between the two sexes for now), the group selected as parents of the next generation had a mean weight of 2400 grams. The phenotypic superiority of the chosen birds over the average for their

generation, or the so-called *selection differential*, is then 400 grams. This does not mean that their offspring will exceed the previous generation by that amount. Since the heritability of body weight is .4, only this fraction of the selection differential will be added to the previous mean. The balance can be considered to have been due to non-genetic (or non-additively genetic) sources. Hence we may expect gains from selection to be $400 \times .4$ or 160 grams. The average body weight of the offspring of the selected parents will be $2000 + 160$ or 2160 grams.

The Efficiency of Family Selection

What will family selection accomplish under the same circumstances? The reason that the family is brought into the discussion is that it provides additional information regarding an individual's genotype beyond what is obtainable from its own phenotype. We said that full sisters bear to each other a genetic relationship of .5. Half of the genes which are heterozygous in the population are then held by them in common form. This is the same as saying that the determination of a bird's genotype by the phenotype of her sister is one half of the degree of heritability. Thus if we were to assess the genotype of a female from the phenotypic performance of one of her sisters, we would be only half as accurate in our judgment as we would have been had we used her own phenotype for this purpose.

But when we have more than one sister as a base for our attempted evaluation, our accuracy is increased. We may expect that the environmental forces affecting the genotype of each individual sister will operate at random: they may reduce the phenotypic expression of one sister below its true genotypic merit and they may increase it above the genotypic worth in the case of another sister. The more sisters there are in the family, the better is the chance that the environmental influences will cancel each other out. If we had an infinite number of sisters their phenotypic average would correspond exactly to their genotypic average. This would, of course, give us perfect accuracy so far as a family average is concerned, but it would still be less than perfect for evaluation of the genotype of any one of the sisters in the family.

We can now show that the use of the family average increases the accuracy of selection in accordance with a formula which looks complicated but is really simple. If we call the heritability of a trait h^2 , the genetic relationship between the members of the family r (equal to .5 in the case of non-inbred full sisters), and the number of individuals in a family n , then the accuracy of identifying genotypes from family averages is

$$\frac{nrh^2 + (1 - r)h^2}{1 + (n - 1)rh^2}$$

times the accuracy obtained from individual records.

Let us take the case of full sisters, and substitute for r the value .5. The formula now becomes

$$\frac{.5nh^2 + .5h^2}{1 + .5(n-1)h^2},$$

or, more simply,

$$\frac{(n+1)h^2}{2 + (n-1)h^2}.$$

Now, suppose that each of the families contains five sisters and substitute the number 5 for n . We get

$$\frac{6h^2}{2 + 4h^2}.$$

All we need to know now is the heritability of the character in question to determine whether full-sister family averages are more accurate than individual records. For body weight, where h^2 is .4, the comparative accuracy of individual to family records (with five sisters per family) will be as .4 is to

$$\frac{6 \times .4}{2 + 4 \times .4},$$

that is, as .4 is to .67, or approximately as 1 to 1.7. If the average number of sisters in a family is increased to 10, the comparable ratio will be about 1 to 2.

In the same way we can compute the relative accuracy of half-sister averages ($r = .25$) and of progeny tests (r between parent and offspring = .5).

Individual and Family Selection Compared

The figures obtained so far do not tell the whole story. They do indicate the relative accuracy of genotype identification achieved by the use of different selection methods, but they do not answer the question, which of the two methods is actually more efficient. They do not because the genetic gains possible depend not only on the accuracy of genotypic identification but also on the intensity of selection used. Thus, in the example for body weight, we found that the genetic gain from individual selection will be 160 grams when the selection differential is 400 grams. Obviously if the selection differential were only 200 grams, the gain obtained would have been only 80 grams.

The selection differentials possible under individual selection are greater than those under family selection. Consider a flock of birds averaging 2000 grams and ranging from 1400 to 2600 grams in body weight. When selection is based on the individual phenotypes, it should be possible to choose enough birds to produce next year's flock from those weighing 2300 grams or over.

The average weight of the birds chosen will be, say, 2400 grams, and so the selection differential will equal 400 grams. But if we consider family averages, the range of variation will not be the same 1400 to 2600 grams. Since environmentally induced deviations from genotype will tend to cancel each other out to some extent, it is more likely that the best family will have an average of only 2350 grams and the poorest 1650 grams (the actual range will depend on the number of sibs in a family). To choose on the family basis the same percentage of the flock which was needed for reproduction in the case of individual selection, it may be necessary to use families averaging as low as 2100 grams, as against the lowest individual weight of 2300 grams. The average of the selected families will thus be lower than the average of individuals selected by the first method. Consequently, the selection differential now, instead of being 400 grams, may be reduced to something like 250 grams.

The use of family averages instead of individual records thus has two effects on selection: it increases the accuracy of choosing superior genotypes, but it reduces the selection differential. There is a formula for computing the joint effects of these two factors which we can use to make the comparison between the overall efficiency of individual and of family selection. According to this formula, for full-sister families the gains obtained from individual selection will be to those obtained from family selection as 1 is to

$$\frac{n+1}{\sqrt{2n[2+(n-1)h^2]}}.$$

With families of five each, the formula becomes

$$\frac{6}{\sqrt{20(1+2h^2)}}.$$

Similarly, with families where n equals 10, we have

$$\frac{11}{\sqrt{40(1+4.5h^2)}}.$$

In the case of body weight, where h^2 equals .4, the two respective family sizes lead to ratios of 1 to 1, and 1 to 1.04. It would seem that when the degree of heritability is as high as .4, family selection does not offer any greater efficiency than what can be gained from individual selection.

But when we consider characters with lower heritabilities, the results are somewhat different. Suppose the trait in question has an h^2 of .1. Family selection based on five sisters will be 1.23 times as efficient as individual selection. Selection based on ten-sister families will be 1.45 times as efficient. The reader might find it interesting to figure the effect of family size and heri-

tability on the comparative efficiency of the two methods. He will find, in general, that progeny testing and full-sister family selection, in cases where between five and 10 sisters appear in a family, will be more efficient than individual selection when the heritability is *lower* than it is for body weight. (Larger full-sister families may lead to complications because they will invariably require a prolongation of the hatching season, which increases the *E* fraction of variation and so lowers heritability.) He will also discover that when heritability is *higher* than .4, family selection may be less efficient than individual selection and cannot be recommended in place of it.

Combination Selection

It is easy to see that by combining information from an individual and from its immediate relatives, we could get greater efficiency of selection. Here is a formula for full sisters which gives the ratio of gains to be expected from the best combination of family and individual records. The combination gain will be

$$\sqrt{1 + \frac{(n-1)(1-h^2)^2}{(2-h^2)[2+(n-1)h^2]}}$$

times as great as the gains from individual selection alone. This general formula assumes no *C* effects. Note that the ratio will be at least 1 to 1.

Again we suggest that the reader investigate the efficiency of combined selection as against the other types, by substituting in the above formula different values of *n* and *h*².

To conclude: The choice of a selection method hinges on the degree of heritability of the trait selected for. When it is high (around .4 or more), individual selection is a satisfactory method, and becomes more efficient than family selection as *h*² rises. When it is low, combined selection is indicated for traits where combined selection is possible, and family selection for traits where it is not (egg production in males, and to some extent viability).

There still remains the question of how combined selection is to be carried out. The formula just given refers to the *best* combination of family and individual records. How is this combination arrived at? In other words, what is the relative amount of attention a breeder should pay to individual and to family averages?

The Weighting of Family Averages

The theory underlying this question is complex. We will simply give another formula as a guide. This must be presented in two forms, a simplified form for the more usual cases where no *C* effects are present, and an example illustrating situations with *C* effects. In the first instance, the weight

of the family average as compared to that of an individual record is expressed by the ratio

$$\frac{nr(1-h^2)}{[1+(n-1)rh^2](1-r)}.$$

Thus for a character with a heritability of .05, the average of full sisters (where r equals .5) should be given the weight of

$$\frac{n \times .5 \times .95}{[1+(n-1) \times .5 \times .05] \times .5},$$

or, more simply,

$$\frac{38n}{39+n}.$$

To illustrate the use of family average weighting: Suppose the character considered is the hen-housed average (the production index), which indeed has an h^2 of .05. We wish to decide which of two hens is to be preferred for breeding purposes: hen *A* with a record of 300 eggs belonging to a family of six full sisters (including the bird herself) with a production index of 200 eggs, or hen *B* with a record of 250 eggs belonging to a family of four full sisters with an average hen-housed production of 240 eggs. The comparative breeding value of each of these birds can be expressed by an index which consists of the family average, given the weighting suggested above, *plus* her own record. Further, the records must be expressed in relation to the flock average. Thus, if the flock average in our example equals 180 eggs, the index for bird *A* (substituting 6 for n in the formula) is

$$\frac{38 \times 6}{39 + 6} \times (200 - 180) + (300 - 180) = 5 \times 20 + 120 = 220.$$

For bird *B*, the index value is

$$\frac{38 \times 4}{39 + 4} \times (240 - 180) + (250 - 180) = 280.$$

Apparently bird *B* is to be preferred to bird *A*. Had the record of bird *B* been only 190 eggs (still assuming a family production index of 240 eggs), the figure 280 would have been reduced to 220, so that the difference between representatives of the two families compared would be negligible.

C Effects and Family Averages

The problem of characters which may show *C* effects involves a more complicated expression which right now is not particularly practical to use in poultry breeding. We will give an example because it points out certain pitfalls in breeding systems advocated by those who favor family selection without individual pedigreeing.

Suppose a breeder who wants to improve the production index decides to use a family selection scheme, where the offspring of each male is toe-punched and housed separately so as to avoid individual trapnesting. In other words, he will have no individual records and will rely solely on family averages. Each family will consist of a mixture of full and half sisters in which the average genetic relationship (r) will be about .25. If there are 50 such birds in a pen, the general formula for the family weighting factor which takes into account the possible C effects is, for the production index, approximately

$$\frac{10 - 45c^2}{1 + 33c^2}$$

where c^2 stands for a fractional value comparable to h^2 , in that it measures the proportion of the total variation attributable to C effects, just as h^2 measures the proportion traceable to genetic differences or G . When there are no significant C effects, c^2 equals zero, which means that the family should receive about 10 times the attention paid to the individual.* Of course, with the system of selection proposed, the individual will receive no attention at all except from the standpoint of whether it lived or died, since this is the only type of information which will be available for any given bird. The point is that a *positive* value for the family weighting factor confirms what common sense would suggest: that it is best to breed from the families with highest production indexes.

Now suppose that because of housing conditions, environmental influences have become more common to members of one family than to members of different families. This could readily happen if, for instance, a severe attack of coccidiosis or another disease affected some houses while others escaped. If this type of variation accounts for nearly a quarter of the total variation ($c^2 = .22$), we may substitute the value .22 for c^2 in the above formula.† The numerator will become zero, and so the whole expression will be zero. This, of course, means that under the specified circumstances the phenotypic family average is no guide whatsoever to evaluating the family genotype.

A more extreme case where c^2 is higher than .22, say .5, will result in *negative* values for the family average weighting factor. In other words, when environment is deliberately made more uniform for members of a family than it is for the flock as a whole, it might mean that members of the poorer families are to be preferred to members of better families as parents of the next generation!

* This is the same result that we get when $n = 50$, $r = .25$, and $h^2 = .05$ in the previous weighting formula.

† Actually under these circumstances h^2 itself will be reduced below the given value of .05. But this a rough example and the difference does not matter.

This sounds completely unreasonable. Yet we can give an example in actual field practice. Suppose a purchaser of chicks has a choice of buying them from one of two flocks. One of them has not been exposed to lymphomatosis and the incidence of the disease in it is therefore zero. Another flock has had a history of lymphomatosis so that some selection for resistance to the disease has been practiced. It may still have an incidence of 10 per cent, and thus *phenotypically* show poorer performance than the first flock. Few breeders who have considered the matter will deny that the prospective purchaser should be advised to buy his chicks from the second flock, especially if the purchaser himself knows that his premises carry the infective agent. Yet this advice represents the same sort of paradox that we have just described, since each of the two flocks may be viewed as representing a family of birds.

How often such a situation may actually come up in practice is not known, but obviously the breeder must be on guard against selection methods which may lead to such difficulties.

Selection Criteria

The second problem of selection procedure is the type of measurement to be applied to the birds under selection. As a rule the poultry breeder tries to use as a criterion of selection the very trait which he is anxious to improve. If he is interested in raising the average body size of his birds at the age of 12 weeks, he will use as his selection criterion body weight obtained at that age. But sometimes he may find it more economical to use, instead of a direct measurement, a related one.

For instance, a breeder attempting to raise the average annual production may, instead of trapnesting his birds every day in the year (this is the direct measurement of the trait under selection), trapnest them only five days a week. His objective is to improve the seven-day-a-week production, yet the indirect measure he uses is so closely correlated with the direct one that he can afford to sacrifice some accuracy of measurement in order to cut down his expenses. Indirect selection for egg size is even more striking. It can be shown that selection on the basis of egg weight in the first November of life is as efficient as selection on the basis of spring egg weight, for which improvement is sought.

The extent to which an indirect measure is useful depends on how close is its correlation to the trait under selection. It is reasonably safe to say that five-day-a-week records are closely enough correlated with full annual records to make their use worth while. But can the five days a week be cut down to four? Three? Perhaps one? On these points we have no complete answer as yet, but it is quite clear that the hatcheryman or breeder who carries the

process of reduction to the end by eliminating trapnesting altogether is on very shaky ground. The indirect criteria which he can use, like breed type, conformation, head points and so forth are not correlated strongly enough, if at all, with production records to enable him to carry out much improvement in the production record.

This point needs no emphasis for the specialized breeder. The multiplier of improved stock or the hatcheryman, however, often labors under the idea that physical selection for improved egg production can be effective. The fact is that so far no genetic correlations between any specific body measurement and production records have been discovered. It is true that periodic examination of birds can lead to an estimate of their productive capacity. The identification of a laying state in a bird at an early age can be interpreted as evidence for early sexual maturity; lack of neck molt in the winter months as a reasonable sign of the lack of tendency to long winter pausing; and so on. Yet even careful periodic examination of birds will not lead to any great accuracy of discrimination of various degrees of genetic merit, and in males it is virtually of no value. At best, breeding policies based on such extremely indirect criteria of selection may maintain stock quality, but have no powers of improving it beyond the minimum economic standards of farm production.

Part versus Full Production Records

One kind of indirect selection which can be of utmost value in breeding for improved egg production is the use of part-year records as a measure of the full annual production index. The part-production index from beginning of lay (in spring-hatched birds) to January 1 bears a high genetic correlation with the full-production index. It is true that its accuracy in determining the genotype for the production index is only three quarters of the direct measurement itself. But there are many compensations. One of these is the tremendous saving of labor costs which can be made by suspending trapnesting of all but the birds selected for breeding after January 1. Another is the fact that the indirect measurement becomes available nearly a year earlier than the direct one. Thus birds selected on the basis of their production index to January 1 may be used in breeding when they are one year old, whereas birds selected on the basis of their full record cannot be placed in the breeding pen until a year later. If breeding progress is measured in terms of years rather than in terms of generations, this procedure would double the rate of improvement were accuracy of selection preserved. But even when accuracy is cut by a quarter, the net advantage is obviously on the side of the indirect or part measurement.

The above example illustrates some of the problems of choosing between *sib* and *progeny* testing. It so happens that the progeny test in the limit (when

the number of offspring is infinite) is a more efficient measure of the genotype of a bird under test than the sib test. But the progeny test takes a longer time to complete, while information on contemporaneous sibs becomes available as early as information on the bird itself. The data on the progeny test cannot be used until the bird has been selected first on some other basis, mated, and the offspring subjected to test. This is why the *efficiency* of gains per year is greater with the sib test than it is with the progeny test.

This does not mean that progeny testing has no uses. The most efficient system of improving the production index has been found to be one in which a small amount of progeny testing is used. Thus, when the progeny test is itself based on part records, it may be profitable to include about 10–15 per cent of progeny-tested birds in the breeding flock. The precise proportion matters little. It can be zero or 25 per cent if the occasion calls for it. But higher figures will usually tend to reduce the rate of annual improvement in most traits in which a poultryman is interested. The breeder's best judgment will determine the value of the progeny test to him. It is not essential where individual and sib selection are combined. It can be taken advantage of when genotypes of exceptional merit are identified. The key to the success of a selection scheme is in flexibility of this sort.

Selection for Several Traits

So far, we have tried to find a selection criterion for the breeder who wants to improve a single trait, or an aggregate of traits which can be expressed by a single measurement. As every poultryman knows, few if any breeders can in practice limit their objective to a small number of solitary characters. A breeder of birds for egg production must consider not only the number of eggs, but also viability ("livability"), egg size, breed type (if his customers demand it), and a variety of other factors. A breeder of birds for meat production has to include rate of growth, conformation, rate of feathering and other traits in his overall improvement goal. Furthermore, both breeders must consider characters which may be of no interest to their customers, but which determine the efficiency of their own operations, like fertility and hatchability.

These many objectives pose a problem as to the best means of combining them in a breeding program. Let us say at once that the greater the number of traits selected for, the lower the *intensity* of selection can be for each trait. Suppose that in order to maintain his flock at constant size, the breeder must use 10 per cent of the females in his flock as parents of the next generation. This is the same as saying that he expects to produce an average of ten females from each dam. It does not matter whether this figure is an over- or under-estimation. On the basis of whatever tests the breeder desires to use (in-

dividual, sib, or progeny) he can select the top 10 per cent of his flock for the character under selection, let us say egg number. However, if adequate egg size also forms one of his breeding objectives, he will of course find that the top birds for egg number will not be the top birds for egg size. Even if we make the conservative assumption that egg size and egg number are independent of each other, we can still expect only one out of each ten high-record females selected to be in the top 10 per cent of the flock for egg size. If the breeder wants to combine selection for both traits he will have to reduce his selection standards for each.

In our example the best 10 per cent of the birds in a flock may average (on the basis of survivors' records) 70 eggs above the flock mean. If, however, the breeder also pays attention to egg size, he may find that the birds found adequate for both traits will exceed the average of the flock by only 35 eggs in the egg record. This means that the selection differential instead of being 70 eggs is now only half that. If the heritability of survivors' production is taken at .3, the expected gain in the flock average in the first instance would be $70 \times .3$ or 21 eggs. In the second, the gain would be reduced to $35 \times .3$ or about $10\frac{1}{2}$ eggs. Every time another objective is added to the selection program, it means further reductions in gain.

The amount of the reduction will depend among other things on the closeness of correlation between the desired traits. In our example we assumed that egg number and egg size are independent characters. Actually, in some flocks there is a negative correlation between them which means that the reduction in gain would be even greater than the amount given.

This situation leads us to a fundamental rule for breeders: *the smaller the number of characters concerned in a selection program, the greater the expected gains in each*. The importance of this rule cannot be overemphasized. It is this which should make the breeder think twice before he includes characters with no economic importance in his breeding program. Everyone will agree that a flock of Single Comb White Leghorns, each member having five well-defined comb points, no more and no less, looks more attractive than a flock widely varying in this respect. But every bit of attention paid to such characters will in the long run lower the rate and efficiency of improvement in the economically valuable traits. We assume that most breeders are primarily interested in these.

Less obviously irrelevant traits than comb points are other characters entering breed standards and culling guides, such as plumage color, breed type, and standard defects and disqualifications. So far as we know, they bear little or no relationship to the productive qualities of birds. Yet the commercial poultryman who is the breeder's direct customer often evaluates his stock on their basis. Poultrymen with this viewpoint are the only reason why breeders might be justified in paying any attention to extraneous non-

productive characters. As soon as the commercial poultryman gets convinced that it is the viability, egg or meat yield and quality and not breed points which determine whether his balance sheet shows profit or loss, the breeder will no longer be obliged to include uneconomic traits in his selection procedures. The example of the American Dairy Cattle Club, which judges the merit of breeding stock entirely on the basis of economic traits, might be worth looking into in the field of poultry.

Total Score Selection

In the meantime, even when considering economic characters only, the breeder has a difficult task. Three different methods of proceeding with selection for many traits can be used. They are: (1) selection for one character at a time, (2) simultaneous selection for several characters on the basis of separate standards for each, and (3) so-called *total score selection* on the basis of a single criterion combining all the desired traits.

It can be shown that the third method is more efficient than the first two, at least in theory. We will limit our discussion to it.

An ideal total score is a selection index incorporating information on the individual and family performance on every trait to be considered. In such an index, each measurement would be weighted in accordance with three factors: (1) the economic contribution each character makes to the overall worth of a bird, (2) the heritability of each character, and (3) the extent to which each of the desired traits is correlated with the other traits under selection.

It is clear why the first two factors must be taken into account. The more important a character is economically, the more attention it should receive in a selection index. The greater the heritability of a trait, the faster are the gains which can be obtained from selection. The third factor is less simple and calls for an illustration.

Suppose we are interested in improving the conformation and rate of growth of a flock devoted to broiler production. Body weight at 12 weeks of age, breast width and keel length may be our three desirable traits. Now it so happens that a positive genetic correlation exists between body weight and keel length. This means that if we selected for body weight alone, keel length would also increase as a result of the common genetic control of both. In one flock of New Hampshires it was found, for instance, that in selecting for body weight every additional unit increase in body weight would automatically lead to an increase of .8 units in keel length.* Similarly, in selecting on the

* The units referred to here are not pounds and inches, but rather *standard deviations* (a statistical constant). In the New Hampshire males in the flock discussed, one standard deviation in 12-week body weight equals about eight ounces, while one standard deviation in keel length is about one quarter of an inch.

basis of keel length without attention to body weight, a gain in one unit would result in an increase of .8 units in body weight. The correlation between the two traits is so high that if attention is paid to one, the other need not be weighted too heavily in the selection index, because a good share of the possible gain in it would be made automatically.

Much less convenient for the breeder are desirable traits between which negative correlations exist. This is the case for keel length and breast width. A negative correlation means that when selection for increase is practiced for one of them, the flock average for the other will decrease. No selection procedure can entirely overcome the conflict of negative genetic correlations. The *purpose* of a selection index is to find the most profitable balance between the pulls exercised in opposite directions by negatively correlated characters under selection: so that while the gains in respect to each will not be the greatest possible, the gain in *total economic worth* will be.

Selection Procedures

Making selection indexes is a complex job, and it is out of the question for each individual breeder to undertake a special index for the special conditions of his own flock. Even in experimental flocks the work is so great that no complete index for any comprehensive breeding project has as yet been made. However, certain clues and guides are beginning to be available for several types of breeding projects.

As one instance, it was found that if the main object of selection was breast width in the flock of New Hampshires mentioned, the fastest gains could be expected when an index incorporating body weight (W), shank length (S), keel length (K) and breast width (B) took these proportions:*

$$\text{Index of breeding worth} = W + 2/3B - 1/5S - 1/5K.$$

This, however, represents a relatively simple situation where improvement in breast width is wanted, perhaps at the expense of other valuable traits not considered in the index (for instance fertility, which may or may not be affected by changes in breast width). Besides, this index is intended for use under individual and not combination selection, though the heritability of breast width is in the range where some attention to family averages may be profitably given.

In general, it is premature at this time to recommend any particular selection index for commercial use. But the principle involved can definitely be put to good use, particularly by breeders for egg production. This is because the two main characters such breeders are vitally interested in are egg num-

* The measurements are in kilograms and centimeters. Other units, such as pounds and inches, would call for different fractions in the index.

ber and viability. The breeder can select for each trait separately or he can base his selection procedure on the combination of both. The hen-housed production average, or as we have called it, the *production index*, is not necessarily the ideal combination where precise weighting is applied to each component, since it is not weighted for the heritabilities of the two components; but it does represent an approach to the total score. As such, the use of the production index is a more efficient plan of selecting birds than separately considering viability and egg records of survivors.

This fact can stand emphasis. Some breeders have objected that selection on the basis of the production index would lead to increased mortality and loss of "stamina." This argument does not carry much weight when we realize that it is the balance sheet which is important to the producer. The production index gives the best approximation to it (except where the meat value of culls contributes an important share of the poultryman's income). It provides for the most profitable balance between viability and egg number. Neither of the traits will be permitted to drop below an economically sound level. This is quite likely to happen when undue attention is paid to one or the other. The mortality rise of the 1920s and 1930s (when individual selection for high egg number was in vogue) may well be an example of such a case.

All of this, of course, refers to selection on the family or combination basis, since the production index as a selection criterion can have but little meaning when applied to individuals alone.

If we consider viability and egg number further, we see that each of them is in itself an aggregate of still further characters. Thus, the mortality level of a flock may represent the net combination of resistances and susceptibilities to various diseases. The survivors' egg record is the result of different potentialities, such as rate of sexual maturity, the tendency to pause in the winter, the extent of the broody instinct, the ability to maintain a laying state into the period of the normal annual molt, and the rate of laying. The production index has the virtue of combining all these diverse factors into one figure, to which selection can be applied.

One adjustment in the use of the production index may be suggested. It so happens that when appropriate weighing for heritability and economic contribution is made, early production seems to be more important than late production. The average performance to January 1 can then be profitably given extra attention beyond what is given to the total annual record. This fact further supports the use of part records in selection, and incidentally illustrates the wisdom of several earlier generations of poultry breeders who based their selection procedures on winter records in preference to spring ones.

As breeding objectives change, selection indexes are bound to change also. At the moment, the only practicable application of the total score idea is to

use the production index rather than survivors' records and viability separately, and, all other things being equal, to give preference to families and birds with higher production indexes in the first rather than in the last half of the laying year.

This recommendation must be qualified too. For instance, a survey of results from laying tests indicates that the stock of some breeders may perform adequately at the beginning of a test but cannot maintain the pace, and go to pieces in the summer. Possibly these birds are deficient in genes responsible for high persistency of production. Under these circumstances more attention may be given to the performance in the summer and second fall of laying than we have suggested. In general, the type of total score, or approximation to it, which a breeder uses as a criterion of selection must be dictated by his specific needs. No single index will apply for all flocks.

Selection and Culling

There is one more point about selection: the culling of flocks under test. The no-culling provision of many official improvement schemes has always been a thorn to breeders. In the United States and Canada compromise solutions have at times been reached, when breeders were permitted to cull birds or families of birds in the early stages of the laying year. In Great Britain, the no-culling regulation of a recently inaugurated improvement scheme raised a storm of protest from breeders who did not want unthrifty birds in their flocks, thinking that maintaining them in the laying houses would make the scheme economically unworkable.

The no-culling provision will indeed raise the cost of the breeding program. But there is good indication that the increased accuracy of identifying the desirable genotypes from uncultured flocks may more than offset the added expense. A precise answer to this problem is not yet available. Perhaps we may eventually reach a compromise between the two extreme viewpoints. Available evidence in the meantime favors the no-culling scheme.

Let us take a possible example. Suppose we have two families of five birds each with uncultured production records as follows (a *d* indicating that that bird died in the course of the laying year) :

<i>Family A</i>	<i>Family B</i>
250	300
240	250
230	200
180d	70
100	40d
—	—
Average: 200 eggs	172 eggs

On the basis of an uncultured population, the average of family *A* is clearly superior to family *B*. Now suppose that the bottom two birds in each of the families could be identified beforehand by an expert culler as inferior, if, say, they showed unthrifty appearance due to the onset of disease. When such birds are culled and their production records eliminated, the family averages of the two groups will read in the breeder's summary—

Family *A*: Average 240 eggs 2 culls

Family *B*: Average 250 eggs 2 culls

—or, if zero production is assigned to the culls—

Family *A*: Average 144 eggs

Family *B*: Average 150 eggs.

To look at such a summary, family *B* is superior to family *A*. But this is not the case. It is, of course, to some extent a speculative matter which of these two particular families actually has the better genotype for hen-housed production. But *on the average*, among a large number of *A* and *B* families, greater genetic improvement can be expected in breeding from the *A* families, not from the *B* families. In this way we can see that culling procedures may obscure true genetic worth. Culling procedures also add an extra character (percentage culled) to the production index, and this reduces the efficiency of selection for the index.

There are technical difficulties in applying a no-culling rule. Some date or age must be selected as the base point from which the production index is computed. From the breeder's standpoint the date of hatch may not be the best choice, since much pre-laying mortality is accidental in nature (that is, the heritability of chick viability in some flocks seems to be low). Use of the original number of pullets hatched as a base for the family average is therefore not recommended. The choice of any other starting point in the life cycle of a flock is arbitrary, and only a compromise solution of the problem is possible. In some flocks six weeks of age, and in others five months, are the points selected. Whether these are the best possible choices is difficult to say. It is probably wisest to use a date or age not later than the beginning of lay of the earliest maturing bird in the flock. From the commercial producer's standpoint, on the other hand, comparison between different flocks may best be made on an overall basis: from the day-old stage to the final disposal of the birds.

What we are saying about culling applies, of course, to flocks on which data are being gathered for future use in selection procedures. For other purposes culling may be economically desirable. For instance, in the breeding scheme described on page 22, there is little reason why pullets should not be culled after January 1. Trapnest records beyond that date will not be

taken. Culling in this case does not destroy the sample on which decisions about the genotypic merits of a bird or a family are to be made. It is true that the annual production index by which the breeder judges his progress in genetic improvement cannot be considered an accurate measure under such circumstances. But the breeder must choose here between perfect accuracy and lower costs of operation.

Mating

Mating Systems

After the breeder has selected from his flock the birds which are to become the parents of the next generation, he has to decide what combinations he is going to use in mating them. There are several systems he is free to follow.

First, he can mate birds at *random*, and assign the chosen females to the pens headed by different males simply by chance.

Second, he can mate females he considers to be best to his best males, and the poorest of the selected birds to the poorest. In other words he can mate like with like. This system is known as *somatic assortative mating*.

Third, he can use the opposite of the previous process and mate the best birds of one sex to the poorest of the other. This is *somatic disassortative mating*.

Fourth, he can mate together closely related individuals, that is, he can use *inbreeding*. The fifth method, *genetic disassortative mating*, is the opposite of inbreeding. In its limit it cannot be used within ordinary isolates and calls for crossbreeding. In a closed flock of a single breed, genetic disassortative mating reduces itself to random mating with restrictions. This will become clear as we go on.

All of these systems can be used in individually pedigreed, pen-pedigreed, or flock matings. Our main interest is with individually pedigreed and to some extent pen-pedigreed matings. But the genetic consequences of the first kind in the main apply to the others as well and we shall not consider them separately.

Each of the five systems can be varied and modified. For example, restricted random mating may be based on the chance combination of males and females with a proviso that no full sisters be placed in a breeding pen headed by their brother. This restriction can be extended to half sisters, cousins, or whatever other degree of relationship the breeder wishes to set as a limit between mates, without unduly affecting the essential randomness of his breeding pens. A practical method of restricted random mating which has been used in some flocks is based on pedigrees to two generations (ending with grandparents). In this scheme only birds having no common grandfather or grandmother are to be mated together.

Somatic assortative mating can have a variation where the best are mated to the best not on the basis of the overall criterion of selection, but from a consideration of component factors. For instance, in the case of breeding

for improvement in the production index, early maturing birds may be mated together in one pen, non-pausing birds in another, and so forth without regard to their production index (after they have been selected on its basis).

Likewise, the somatic disassortative method can take the form of compensatory mating, in which the defects and excellences of the two mates are balanced. Thus, a bird possessing good egg size but showing winter pause could be placed in a pen headed by a male judged to come from a small-egg-size but non-pausing family.

Inbreeding can be of varying degree or intensity. Full brothers and sisters can be mated together, or half brothers may be mated to half sisters. Other variations on the same theme may be adopted in a systematic fashion, or less formal schemes of mating relatives together may be used. What is known as *linebreeding* is also a form of inbreeding, in which an attempt is made to increase the number of times a given bird appears in a pedigree by the mating together of its descendants.

We need not consider genetic disassortative mating in any detail. When it becomes wider than restricted random mating it usually stops being a method of genetic improvement. Our remarks about migration (page 12) apply here as well. Crossbreeding as a system may produce superior stock in the first generation of a cross, a fact recognized and used by producers of birds for meat. But the improvement from generation to generation must depend on the selection and mating schemes followed *within* each of the breeds. Only when an attempt is made to synthesize a new variety from crosses between two or more previously existing ones is genetic improvement involved. Such attempts are the concern of a very small group of adventurous breeders. They are subject to special requirements and conditions in each instance. We can give no general instructions for the best methods to cover all cases, and by and large the whole problem lies outside our subject.

We will therefore compare the first four mating systems only. None of these is perfect for all purposes. There are advantages and disadvantages to each, and most likely the best procedure will be a flexible approach, using various combinations between them. This statement is not likely to satisfy breeders who want practical instructions. On this account we will briefly show the merits and dangers of each system, aiming at a practical recommendation not for the best method, but for the most workable one at the present time.

Inbreeding

Inbreeding for years has had and still has many enthusiastic supporters, who may not always see the consequences of their recommendations. To start with, intense inbreeding is the only one of the mating systems which

has any powers of fixing traits that depend on many gene pairs for their expression. But we have already pointed out that when characters of relatively low heritability are dealt with, fixation in the sense of achieving complete uniformity is not possible even if desirable (which also is questionable). Further, we have noted that under inbreeding non-additive genetic effects enter the picture. Under random mating the knowledge of the selection differential and of heritability permits prediction, within the limits of sampling error, of the average level of a trait under selection in the next generation. But when non-additive genetic action enters the picture, this is not possible.

Particularly distressing is the fact that non-additive effects in inbred stock lower the performance in productive characters. Numerous experiments conducted with poultry have shown that intense inbreeding with or without selection cannot raise the productive level of economically valuable traits. Some supporters of intensive inbreeding as a method of fixing characters may dispute this. We suggest that they look at the recent literature on genetic theory and experimental inbreeding in species other than poultry, literature which leaves very little room for doubt on the matter. Or let them search their own experience and find a single instance where inbreeding has been able to *fix* egg production, viability, or hatchability at a *high* level of performance in a flock or strain.

Why, then, do we need to consider inbreeding at all? For two reasons. One concerns forms of inbreeding less intense than those involving full brother x sister or half-brother x sister. The second is the production of inbred lines for the purpose of subsequent crossing.

Moderate Inbreeding. At present it seems that the degree of inbreeding to be gotten by restricted random mating (page 31) is not necessarily detrimental to the performance of the birds. There may be some question whether more homozygous birds are produced by such a method than by ordinary random mating. The fact is that so far as pedigree relationships are concerned, some inbreeding does occur under this scheme. In the breeder's hands it may be reasonably useful for special purposes.

For instance, a breeder may find that without previous warning an anatomical defect has appeared in his flock. This may be a character easy to identify, like crooked toes in day-old chicks, or it may be a more serious condition which kills the embryos before hatching (a *lethal* gene or combination of genes). In such cases the breeder may try to eliminate the genes responsible by applying intense selection to his flock against the undesirable trait. But if the trait is recessive, it may be that the culprit genes have spread widely throughout the population before being noticed. The breeder's problem may then be to fix the desirable counterparts of the undesirable genes. This is of course what is meant by selection against an undesirable trait. But the point is that fixation as noted may call for some inbreeding if the unde-

sirable gene is present in the majority of the flock. A judicious combination of selection with mild inbreeding may have to be brought into action under these circumstances.

Inbreeding may serve a further purpose as an incidental process in selection. A breeder who has identified a superior genetic combination by whatever means (sib or progeny testing) should naturally try to take advantage of its existence in the flock. He may do this by favoring in his selection the individual or family carrying this genotype. If he practices family selection he will find that the number of different ancestors present in the pedigree of his flock will be materially reduced from the number found under random mating. In fact, selection itself will result in a certain amount of inbreeding.

There is a dissipation of genetic worth in every generation by which birds are removed from the desirable ancestor. It is caused by the tendency of superior genotypes to produce offspring which will regress to the flock average, owing to the fact that the superior individual contributes only half of the inheritance received by its immediate descendants. Nevertheless, the only practical method of partial conservation of desirable genotypes in the flock lies in the type of selection, which may automatically involve linebreeding in one form or another.

Hybrid Vigor. The second broad purpose of inbreeding, producing crosses between inbred lines, is part of a vast and complex subject which would take a book to treat. Most poultrymen are now familiar with the ideas behind this scheme, and yet our knowledge of either the proper techniques of putting it into operation or of its efficiency as a method of poultry improvement is incomplete.

The basic fact is that when inbred lines are crossed, the first generation of offspring show what is called hybrid vigor or *heterosis* for some traits. The term heterosis refers to the condition when the crosses are superior to their parents in performance. Usually, heterotic behavior is shown in traits such as hatchability, viability and growth rate, but not in others, like egg size. Of course, one of the reasons why the hybrids are superior to their parents is that the parents, being inbred, do not themselves excel in these particular traits. The question is whether the hybrids are indeed better than the superior strains of birds produced by other selection and breeding methods.

This question has not yet been adequately answered for chickens. We know definitely that in some plants, like corn, the method of crossing inbred lines is an efficient technique for raising yield. But in the light of present information it is too early to transfer this conclusion from corn to chickens, and it will probably be some years before we have a clear solution. In the meantime, even if inbred crossing is as usable and efficient as many believe, it will call for a vast expense of money on the part of the breeder, for specialized direction by highly trained geneticists, and for other requirements

which most present-day breeding establishments would find it hard to meet. Wholesale adoption of it would cause revolutionary changes in the structure of the whole poultry industry.

It is well known that the recent extensive commercial exploitation of the techniques of hybrid chick production has already made heavy inroads into the hatchery business. This is probably all to the good if it leads to the replacement of unimproved flocks by better stock no matter how produced. But whether hybrids or crossbreds will completely drive out *efficient* closed-flock breeding programs is still very much a question. Likewise, we still do not know how promising are several other recently proposed methods, such as the so-called "reciprocal recurrent selection." The answers, of course, are to be sought in impartially conducted research, such as is now being undertaken by many agencies, and not in high-pressure commercial promotion.

Other Mating Systems

The remaining three mating systems in their various forms are of more immediate interest to breeders now engaged in poultry improvement. The genetic consequences of random, somatic assortative and somatic disassortative mating schemes are somewhat different. The first promotes genetic variability, but probably leads to a slower approach to the extreme top levels of performance for the selected characters. The second permits a more rapid extension of the range of performance. The best birds in each generation may be better than the best of the preceding one. The rise in average performance does not, however, keep pace with the extension of the range. The third method, somatic disassortative mating, works in the opposite direction: the upper limit is not extended at a rapid rate but the lower limit of performance may be raised.

The extent of the differences between the three methods depends on a series of factors, such as heritability, the number of gene pairs involved in the inheritance of a trait, and the degree to which heritable resemblances in performance between the potential parents can be recognized.

There are special uses for each method. For instance, in the progeny testing of males, which involves comparisons between the performance of several sires each mated to a group of dams, random mating provides fairer estimates than the other types. When the dams are randomized (when mates for each sire are selected by chance), it is more likely that genetic differences between them will cancel out, so that the average of each sire's offspring may be used as an estimate of his genotype with greater assurance of accuracy than when other mating methods are involved.

Somatic assortative mating should probably be practiced in at least part of the flock if extension of range of performance is wanted. Somatic dis-

assortative mating may, on the other hand, be useful when the middle expression of a trait is preferred to both extremes. For instance, since neither too small nor too large eggs are commercially desirable, it may be worth while to keep a happy medium by mating large-egg females to males with potentialities for small eggs, and vice versa.

The choice of a specific mating scheme must depend on the particular objectives of the breeder. As a rule, it is best not to keep to any formal scheme too rigidly, but to approach the problem in a flexible way. Perhaps in general a combination may be recommended, which will include a random mating system with restrictions so that no female with a grandparent common to the male be placed in his pen, somatic assortative mating for the upper half of the selected flock, somatic disassortative mating for the lower half, and occasional excursions into inbreeding for special purposes.

Practical Applications

The Heritability of Economic Traits

We have so far considered the fundamental basis of inheritance, the principles of selection, and the forms of mating systems. These matters in a general way cover the fundamentals of the breeder's trade. A more concrete application of these principles to actual breeding practice calls for further consideration of the most fundamental of genetic constants—the degree of heritability.

Our information about its size for different economic characters is quite incomplete. It should be realized that the genetic approach to breeding problems which we are talking about is a relatively new one. Less than a handful of experiment stations and institutions have so far contributed to it. Precise information is lacking and in our discussion of actual heritability values we must limit ourselves to estimates, some of which are fairly sure, while others are merely first approximations.

In general, heritability values for different traits of economic use can be classified simply as high, middle, and low. Characters classified as high readily respond to mass selection. Middle characters require a combination of mass and family selection. Characters with low heritability also depend on a combination method of selection, but sometimes it may be found simpler to use family selection exclusively.

Traits with High and Middle Heritability. The breeder interested in improving meat quality is by and large dealing with traits with a high h^2 . Both *body weight* (at various ages) and *rate of growth* have heritabilities of from .40 to .50. It would seem then that family selection for these characters is no more efficient than individual selection. Note, however, that body weight in the early stages of life is to some extent determined by the size of the egg from which a given chick emerges. This will be recognized as a C effect, since full sibs are likely to arise from eggs resembling each other in size. The magnitude of the C factor is gradually reduced as the birds grow older, until only a small C residue is present in mature body weight.

Conformation comprises traits with either high or middle heritability. Thus shank length has an h^2 of about .5, keel length roughly .3, and breast width .2. Shank length, it must be understood, bears a strong genetic correlation to body weight. This means that efforts to increase body weight and reduce shank length within a flock may not only be very difficult, but even in some cases impossible. Selection of equal intensity for both characters is likely to result in a standstill performance for both, and even the best selection index

may not resolve this difficulty. Whether or not there are strains in which the genetic correlation between body weight and shank length is low or non-existent is not known. Only in such groups could the combination of large body size and short shanks be attained.

The negative genetic correlation between keel length and breast width is not high. We have already noted that a selection index to combine the two traits has been constructed for one flock of New Hampshires. The particular point of interest about these two characters is that their heritabilities are low enough to make combined selection preferable to individual selection. This is especially true of breast width.

Another high-heritability trait is *egg weight*. Its value is about .6, which makes possible improvement by individual selection without regard to family averages. About the heritability of other egg characters we know less. In some cases these seem subject to partial control by non-genetic forces relating to the dam. The best established example is shell thickness, but there are also indications for albumen quality. The generally high heritability of egg characters accounts for their rapid response to selection.

We have no exact information about other high or middle h^2 traits, with one exception: *egg production of survivors*. For this character it is almost certain that h^2 is near .3. This figure applies equally well to the annual record and to part-year records (when only birds surviving the first laying year are considered). It is likely that *rate of feathering* in heavy breeds where there is a mixture of slow- and rapid-feathering types in a flock has relatively high heritability. Likewise, the h^2 of *sexual maturity* is in the middle range, somewhere about .2 to .3.

Traits with Low Heritability. Of characters with low h^2 , particularly important are the two for which our information is reasonably precise: the *production index* and *viability*. Both are below .10. The most acceptable present figure for the production index is about .05 and for viability about .08. Both these characters (viability is, of course, a component of the production index or hen-housed average) are extremely important to commercial poultry breeders, whether primarily interested in eggs or in meat. We have seen that mass selection applied to them is not very efficient. The superior method is probably combination selection, with emphasis on family averages but with some attention paid to individual performance. But family selection alone may be profitable sometimes, particularly if precautions are taken about the C factor.

We will say no more about the production index except to repeat that the breeder, whose first concern is not with meat qualities but with eggs, should rely on it as a selection criterion. The formulas given on page 19 can be used to determine what weight is to be given to the family record as compared to the individual one.

About first-year viability more must be said. In general, a breeder who uses hens two years old or older for reproduction permits nature herself to exercise individual selection. There are only two possible phenotypes a bird can have for viability: either she dies during the first laying year or she survives. The birds which die are not available for breeding purposes in their second year. Family selection is therefore the only tool the breeder can use under the circumstances. If his flock mortality is very high, he may find that there is no room left for any selection on his part—he may have to breed from all of the survivors if the flock is to maintain its size. But in general the breeder will have some opportunity of rejecting certain families. The most useful criterion for this purpose is the percentage of survival.

We may note here that when full-sister families differ in size, an equal percentage of mortality does not indicate equal genetic merit. Thus if one out of a group of three birds dies, the survival rate of 67 per cent is not genetically equivalent to the same ratio of living to dead birds in a family of nine pullets. A "conversion formula" to equalize the information for families of different sizes may be applied. It is given as

$$\frac{n}{1 + (n - 1)rh^2},$$

which contains symbols we have already used. For the case of full-sister families ($r = .5$) and viability ($h^2 = .08$), the expression is

$$\frac{25n}{24 + n},$$

where n is the number of sisters in a family. Thus if we tried to decide which of the two families given above is the better, when both come from a flock with an average viability of 40 per cent, we would multiply their respective superiority over the flock as a whole ($.67 - .40$, or $.27$ in both cases) by $\frac{25 \times 3}{24 + 3}$ in one case, and by $\frac{25 \times 9}{24 + 9}$ in the other. Obviously the larger the family the more accurate is the information on its genetic merit available from its average performance. Preference should be given in selection to larger families over smaller families with the same mortality incidence when it is lower than the average.

Often there are situations where particular attention must be paid to a specific given disease rather than to mortality from all causes. An example is the case of lymphomatosis, which at one time caused such severe losses as to have forced its singling out as a specific breeding objective. The heritability of resistance to this disease is about .05 in the flocks in which it was studied. Resistance to other diseases may have lower h^2 values. For instance, the proneness to develop unspecific disturbances of the reproductive system has

such a low heritability (.02) that little progress in the breeding control of this defect may be expected from any but very intensive selection.

Two problems connected with breeding for high viability are of utmost importance but are still not solved. The first is the problem of the correlation between viability and egg number. It seems well established that the phenotypic correlation between the two is positive, that is to say that high egg records are more likely to be obtained where mortality is low. There is a possibility, however, that the *genetic* correlation between viability (particularly that of embryos, that is hatchability) and production may be negative in flocks previously subjected to intensive selection for a high production index, so that intensive selection for improving one of these traits may decrease the average performance of the flock in the other. This, if true, is another reason why total-score selection as exemplified by some form of the production index is to be preferred to selection on the basis of each trait alone.

The second problem for viability is the correlation between resistances to different causes of death. There is some conflict of opinion on this point. In one of the flocks studied, there was, for instance, a reasonably high correlation between resistance to lymphomatosis and resistance to other diseases. In another flock the correlation was rather low. If the first situation is more typical it may be argued that general resistance or vigor genes are involved in the inheritance of the production index. This conclusion may not be true if the low correlation is found to hold. Uncertainty about the question shows how our knowledge of the whole subject is still in its infancy. Much intensive effort and experimentation will have to come before we are able to provide satisfactory answers to all the problems faced by breeders.

Breeding from Pullets

The breeder who wants to use pullets for reproduction is faced with a special problem. In selecting the mothers of each generation when the candidates for motherhood are themselves less than a year old, he runs the risk of choosing individuals which, after producing offspring but before the end of the first laying year, will themselves die. This has often deterred breeders from putting pullets into breeding pens. *Such fears are unfounded as long as family performance is the primary criterion of selection.*

Similar fears do not seem to have disturbed most breeders who use cockerels in their improvement plans. Yet the risk of a male dying before reaching his second birthday is not necessarily smaller than the risk for females. A more decisive point is that the heritability of viability is only .08. This means that 92 per cent of variation in the fate of the birds in their first year of life is non-genetic in nature. So it matters little if the individual bird herself lives or dies. What does matter is whether she is a member of a

family with or without high genetic resistance to death-inducing causes. By the time pullet selection for breeding takes place, a reasonably good estimate of family viability is available. There are exceptions in which certain families may exhibit a characteristically late date of death in the first laying year. But as a rule the genetic correlation between viability to one year and viability to 18 months is high. Because of the gains provided by the shorter period between generations, pullet breeding despite these objections still seems to be a sound method.

To the cautious breeder we might suggest taking out some insurance by raising more chicks than he needs, and discarding or selling the surplus before placing his pullets in the laying house on the basis of the mother's fate at that time. His discards would be the chicks from dams which died between the hatching season and the moving of their offspring to the laying house. In this way the breeder will have two advantages: he can capitalize on the gains produced in the rate of improvement by using pullets, and yet he need not include the offspring of birds which die before completing their first laying year in his flock. It is only fair to point out, however, that the selection differential in such a scheme will be below the maximum possible.

Other Details of Breeding Plans

The heritability of other productive traits is not too well known. Fertility, hatchability, persistency, broodiness and winter pause do not seem at best to have high enough heritabilities to make mass selection efficient. We may hope that in the not too distant future more precise information will be available. At present we suggest that breeders proceed on the assumption that a combination of family with individual selection provides the best opportunities of improving these traits, even if the exact weighting of the two selection bases cannot be provided.

Above all, the breeder should not rely on any rigid idea of selection and mating procedures. His greatest efficiency of operation will come when he can adapt himself to the conditions of the moment. Breeding objectives may change, the price structure of the poultry industry may be modified overnight by changes in market requirements or by government regulation. Families or individuals of exceptional merit may be discovered in a flock. Only when the breeder's system is flexible can he on the one hand protect himself against sudden shifts, and on the other, take full advantage of opportunities which may come up.

Specific details about factors other than heritability could possibly be brought into our discussion. The actual variety of details that each breeder faces is, however, too large for treatment. Often such details call for individual decisions which cannot be made in a blanket fashion. For instance,

there is no best system of record keeping. Each system must answer each man's needs and facilities. It is likewise impossible to say outright whether, as an example, improvement in egg size should be pursued in preference to improvement in persistency, or vice versa. Questions of this sort depend on the particular conditions in each flock and each chick-marketing area. It is difficult to foresee a time when such details can be given rule-of-thumb treatment. The important thing is to understand the basic principles. Once the breeder has understanding, he will be a more competent judge of the best procedure to use than any recognized authority who lack information on the flock in question.

We now turn to some general remarks on the immediate application of our principles to the commercial poultryman's problem of finding good stock. For reasons already given we shall not concern ourselves with chicks produced by crossing inbred lines.

The Commercial Poultryman

Breeding Methods and the Commercial Poultryman

The commercial poultryman who operates either a specialized egg-producing farm or a broiler plant must choose, on the basis of many attractively presented claims, the source of supply of stock. The general farmer of course has the same problem, but his investment in poultry may be modest, his requirements may be met with cheaper chicks, and his annual income depends only to a small extent on the rightness of his choice of stock. To the commercial operator the question is much more serious, for he cannot withstand a succession of serious mistakes and still make his living from poultry.

It is surprising, then, that among the welter of information available to the poultryman on nearly every management problem he may face, there is so little on the vital subject of the choice of supplier. There have been many recommendations made in the past on the choice of breed, but the choice within the breed is at least as important and little has been done about it. The reasoning behind this deficiency seems to be that there is nothing the commercial operator can do about the genetic potentialities of his flock. He may build new houses, change diets, vaccinate his birds, but the inheritance of his birds is fixed before the chicks ever reach him. This is of course the very reason why he should have information on their breeding. Only when he is in a position to discriminate between the claims made for the different sources of supply, can he form any kind of beforehand judgment as to where to buy his stock.

In general there are three types of suppliers on the market: the hatchery, the hatchery-breeder, and the breeder. There are complex degrees and gradations within this simple classification. It is not uncommon for chick producers to call themselves breeders. Should a poultryman simply accept such self-classification? Obviously not, since it is not what the chick producer calls himself, but the breeding policy he follows which classifies him.

In the final analysis the only test which poultry have to pass is that of making money for their owners. No amount of previous information will settle this question. Hence, when a poultryman wants to change his supplier, the best thing he can do is to conduct an experiment. He should buy stock *simultaneously* (not at different times of the year) from both the old and the new sources, provide the two groups with as uniform environment and care as possible, and draw his conclusions from the comparative cost accounts.

Such experiments even on a small scale may be desirable throughout the poultryman's career, because a single source cannot supply chicks of uniform quality year after year, and trends of improvement or deterioration will change the relative values of different strains in the course of several years.

But the commercial poultryman cannot afford to jump blindly at every offer of stock. He must discriminate between the sources worth trying and those obviously unsuitable, or his experimenting will put him out of business. How can he do this?

The sources of information open to the poultryman are reports of other customers, advertising descriptions of selection and mating systems, contest results, and data from government improvement schemes. To advise on the value of the first of these would take the combined services of a psychologist and an economist, and not those of a geneticist. To some extent this is also true of the second source, but here the geneticist may be of some help. The evaluation of the remaining two sources depends on an understanding of the specific details and conditions under which the data were compiled.

Evaluation of Advertising

The advertising of the breeders and the hatcherymen may be based on a combination of the other listed sources of information. The commercial poultryman should pay particular attention to the claims made for the results obtained on the breeder's own premises, and to the description of the selection methods used. Are the production, body-weight, and egg-size averages based on uncultured populations or on selected samples? Do the chicks to be supplied originate from the group of birds described, or from some of their remote descendants with selection suspended in between? What does the breeder precisely mean by family selection and progeny testing? Do they correspond to the systems we have described, or do they simply indicate that the breeder collects the information necessary for such methods without actually using them? Questions of this type are direct, and no breeder can in good faith refuse to answer them. There are no secret methods for improving stock. The available techniques are open to all. The breeder who claims to be in possession of methods he does not wish to reveal very likely has something to conceal.

Many advertisements are based on the virtues of a foundation dam or sire. Outside the fact that pedigrees based on individual performance records are of little worth in the case of egg production (immediate ancestral performance is much more useful, of course, for high h^2 traits), it takes some stretching to believe that chicks of a commercial grade can be supplied in any quantity without a considerable dilution of the supposedly valuable

inheritance of foundation animals. Pedigrees citing family averages are of somewhat greater value, but even they have to be taken cautiously.

In general, an uncultured production average for the supplier's breeding flock is as good an index of merit as the prospective buyers of chicks for egg production can have. Of course, information on factors other than the production index, such as egg size and quality, should be obtained. Not all breeders may be able to supply data on, let us say, the blood-spotting tendency in their flocks, but it is quite correct for the commercial poultryman to make inquiries on such points. The broiler producer, of course, will not be interested in such matters and if, as is usually the case, he buys crossbred chicks, he may inquire about performance tests, not of the parents but of the crosses he is offered.

The breeder's approach to the improvement he is responsible for will often provide worthwhile clues. If he emphasizes high individual records or minimum individual standards for commercial-chick-producing flocks, it is unlikely that he is paying more than lip service to family selection. These words may be unfair to some breeders who feel that high individual records have an appeal to commercial poultrymen. But if poultrymen become convinced that including a 150-egg hen from a 250-egg family in their flock may on many occasions be preferable to using a 300-egg hen from a family with a production index of 100 eggs, the breeder would no longer be under pressure to frame advertising in terms of individual records.

What the commercial poultryman is entitled to get and should demand from the breeder is information on performance and selection standards of the whole flock and not of exceptional individuals in it. The problem is more difficult when dealing with hatcheries or multipliers rather than direct producers of improved stock. There is always some dissipation of genetic merit when a small group of tested and selected birds is expanded into a large chick-supplying flock. The usual methods of culling on the basis of physical appearance do little to stop this trend. The only guide the poultryman then has is an indirect one: it is the breeding policy of the breeder supplying the hatchery itself.

Laying Tests and Official Improvement Schemes

More or less the same things we have said about the breeder's claims apply to contest results and to official improvement schemes. Exceptionally high records at laying tests are of little value to the commercial producer unless he is certain that the stock he buys has been produced by the same methods producing the contest winners. The birds in laying-test pens may, for instance, represent crosses between two strains and exhibit heterosis,

whereas the commercial poultryman may be sold chicks from one of the strains which were used in the cross but which are unexceptional in themselves.

This is why random sample tests of the kind which have been inaugurated in California are of greater value than the usual contest. These tests are designed to measure the production qualities (egg and meat) of commercial stock offered for sale, and not of the breeder's cream of the crop. The reports of the California tests are further useful because they take into account not only production but also costs. The standing of the contestants is determined by net financial returns, not by gross, and net returns are of course the more important returns to the commercial poultryman.

Government improvement schemes in various countries have different bases. Data from them must be as closely scrutinized as data from private sources. A label certifying that a hatchery or a breeder has complied with the regulations of a particular government-sponsored scheme is meaningless unless the provisions of the scheme itself are understood. Very often disease-control schemes are classified under "improvement." There can be no objection to the word so long as it is understood that such schemes do not refer to genetic improvement. Similarly, some schemes or parts of schemes are based purely on physical selection, a method which may prevent deterioration of improved stock to some extent, but certainly cannot produce further improvement. Other schemes may permit culling or preselection of the birds to be entered under government supervision. The commercial poultryman should know the definitions used before he can make use of the reports as a guide for choosing stock.

Conclusion

Our discussion has implied many responsibilities for the commercial poultryman. But it is in his own interest to have them. While many breeders and hatcherymen have a genuine desire to improve the qualities of their stock, they can only afford to undertake elaborate breeding methods if their customers are willing to pay for at least part of the added costs. The extra costs per chick are actually very small when compared to the gains which sound breeding policies can produce. Under present conditions, a gain of ten eggs in the production index of an *average* flock could be readily achieved by investing a very tiny fraction of day-old chick prices. But the incentive for making the investment must come from the commercial poultryman. He is the one to put pressure on the hatchery and the breeder to adopt sound breeding techniques. His understanding approach to the whole question will mean his own benefit and the benefit of the poultry industry.

With help from the poultryman, the breeder and hatcheryman may look ahead to consequences by gradually modifying their respective breeding methods if they are, indeed, inadequate. They can do this only by familiarizing themselves with the genetic principles underlying the processes of poultry breeding. We have noted that there is no one universal recipe that a breeder can follow as a housewife follows a cookbook. Understanding is required first of all. The best breeding scheme will break down if unintelligently used, and even the least efficient one may have some redeeming features if applied with understanding.

Reading

No books designed to acquaint the practical breeder and the poultryman with the intricacies of modern genetics as applied to their field are yet available. A general text, *Animal Breeding Plans*, written by Jay L. Lush and published by the Collegiate Press, Ames, Iowa, discusses most of the important aspects of the subject. But it is intended primarily for students of livestock rather than poultry breeding and is technical. Also technical is *Population Genetics and Animal Improvement* by the present writer (Cambridge University Press) on which much of our discussion is based. The scientific articles published in such journals as *Poultry Science* present the same difficulty.

A rather more general approach to poultry breeding is given in *Poultry Breeding*, by Morley A. Jull (John Wiley, New York). It does not deal with the genetic basis of traits of economic importance as we do, but it is particularly valuable for a descriptive treatment of productive characters and for full reference lists following each chapter.

A later book, *The Genetics of the Fowl*, by F. B. Hutt (McGraw-Hill, New York) is a good source of information on characters largely determined by single-gene-pair differences. But it does not make use of available modern techniques in treating quantitative characters.

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